

The winter foraging behaviour of birds in a mixed eucalypt forest and woodland on the Southern Tablelands of New South Wales

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ABSTRACT

In this paper, I present data on the foraging behaviour of eucalypt forest and woodland birds at two sites on the Southern Tablelands of New South Wales during the non-breeding season (winter). The winter community was a subset of the summer community, with six guilds among 23 species identified by cluster analysis compared with seven guilds among 41 species in summer. Despite this difference, birds were abundant during winter, with more than 200 individuals of 29 species recorded during July censuses on the two 10 ha plots. Although a few birds fed on nectar, nectar was not abundant in winter and the nectar-foraging guild present in summer was absent in winter. Most birds that relied on large arthropods and aerial foragers left the area after summer and an aerial foraging guild was restricted to one species, the Grey Fantail. As in summer, species differed in foraging manoeuvres and substrates, as well as foraging heights and the plant species frequented to find food. The continued abundance and diversity of species/guilds through the winter is best explained by the variety of food resources available for birds; the complexity of foliage, bark, and ground substrates provided a wide range of foraging substrates over the entire vertical profile of the vegetation. Maintenance of this structural complexity is essential for the survival of eucalypt forest and woodland birds.

Key words: Eucalypt forest and woodland birds, community foraging ecology, threatened species, non-breeding season, guild structure, conservation management

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Introduction

Studies on the community foraging ecology of eucalypt forest and woodland birds have been primarily conducted during the spring breeding season (Recher *et al.* 1985; Abbott and Van Heurck 1985; Ford *et al.* 1986; Recher and Davis 1998, 2002, 2010), with studies during the non-breeding season restricted to guilds or groups of species (Wooler and Calver 1981; Recher 1989; Cale 1994; Wheeler and Calver 1996), or to observations made in association with studies focused on bird populations (Loyn 1980, 1985). This is despite the non-breeding season occupying more than half the year for most forest and woodland birds in Australia (Yom-Tov 1987; Marchant 1992; McLean *et al.* 2005).

The emphasis on breeding season studies arises from understanding that breeding birds have strong demands for food for the production of eggs and rearing of young. At these times competition for food and space may be intense, particularly among conspecifics and closely related species (MacArthur 1958). However, the resource requirements of birds outside the breeding season are also significant and occur when food abundances in eucalypt forests and woodlands are less than during spring and summer when most birds breed (Majer *et al.* 2003; Recher *et al.* 1983a; 1996). Rather than diverging in their use of food resources when demands for food are greatest, there is some evidence that species are more similar in their foraging behaviour during the breeding season than during the non-breeding season (Recher 1989). The interpretation is that with limited food resources

during the non-breeding season species specialize on the resources which each is most efficient at using and therefore diverge in how they forage and the foods used.

Regardless of the underlying reasons for similarities and differences in foraging ecology among eucalypt forest and woodland birds, an understanding of the structure of non-breeding communities and their use of food resources is required for their management and conservation. Australian woodland birds are increasingly threatened by human activities that lead to habitat degradation, loss, and fragmentation (Recher 1999; Ford 2011; Ford *et al.* 2001; Rayner *et al.* 2014). In this paper, I present data on the foraging ecology and guild structure of a eucalypt forest and woodland bird community in southeastern New South Wales during winter. Earlier papers described the foraging ecology of this community during the spring/summer breeding season (Recher *et al.* 1985; Recher and Holmes 1986; Holmes and Recher 1986; Korňan *et al.* 2013). Here I compare foraging behaviour and guild structure between breeding and non-breeding seasons.

Methods

Study Sites

The study was conducted on two 10 ha plots (420 m x 240 m), WL1 and WL2, located in southeastern Australia approximately 40 km southeast of the town of Bombala (36.91°S, 149.24°E) near the Bondi Forest Lodge (37.15°S, 149.15°E) at 800–850 m above sea level on the

Southern Tablelands of New South Wales (NSW). The plots were about 5 km apart. Both consisted of regrowth forest and woodland and were bordered by grazed pasture, with WL2 bounded on one side by a Monterey Pine *Pinus radiata* plantation. Both were grazed by sheep and cattle and cut for firewood. The plots formed part of continuous bands of forest and woodland extending several kms through pastoral country, but were separated by pasture, a creek, and sphagnum bogs.

WL1 was divided equally between a Snow Gum *Eucalyptus pauciflora*/Black Sally *E. stellulata* woodland and dry, open forest dominated by Narrow-leaved Peppermint *E. radiata* and Manna Gum *E. viminalis* on well-drained soils and by Swamp Gum *E. ovata* where drainage was impeded. The woodland was heavily grazed and lacked a subcanopy or shrub layer. There were patches of Matt Rush *Lomandra longifolia* and Bracken Fern *Pteridium esculentum*. The forest had an understory of young eucalypts and wattles (Blackwood *Acacia melanoxylon*, Silver Wattle *A. dealbata*), with a shrub layer dominated by Blackthorn *Bursaria spinosa*. Litter was abundant, but there was little ground vegetation. WL2 was an open forest dominated by Narrow-leaved Peppermint and Mountain Gum *E. dalrympleana*, with an understory of small eucalypts, and fringed by a dense regrowth of Snow Gum/Black Sally woodland along one side. There were few shrubs, mainly Blackthorn. The litter layer was sparse, and drier than in WL1, with considerable bare soil. Characteristics of the vegetation are adapted from Recher *et al.* (1985) and summarized in Table 1. Details of vegetation measurement

procedures are given in Recher *et al.* (1985). Additional information can be found in Recher *et al.* (1985) and Holmes and Recher (1986a,b). Korňan *et al.* (2013) provides a link to satellite imagery of the plots via Google Earth. WL3, which was included in the studies of Recher and Holmes, was not studied during the winter.

The Southern Tablelands has a cool, temperate climate. The mean annual rainfall at the Bondi Forest Lodge averaged 992 mm/y from 1930 to 2014. However, it was drier during the study reported here and rainfall at the camp from 1976 to 1981 averaged 820 mm. Mean maximum temperatures from April through July average 9 to 16 °C, with mean minima -1 to 3 °C (Bureau of Meteorology, Station 070226 [Craigie/Bondi Forest Lodge]).

Bird Census

On each plot, birds were counted along two parallel transects 120 m in width and 420 m in length spaced 120 m apart and set back 60 m from plot boundaries. Each transect had an approximate area of 5 ha. One transect on each plot traversed forest, while the other included woodland. We used a fixed width transect procedure described by Recher *et al.* (1983b) to census birds bi-monthly during 1980. Censuses conducted during March, May, and July were considered non-breeding counts, as no nesting or other signs of breeding were observed during those months. The July count was used as a winter census. Each census comprised a two hour count along each transect on four consecutive mornings, weather permitting, for a total of four counts. Counts commenced ~30 minutes after dawn,

Table 1. Vegetation floristics and structure of plots 1 and 2 at Bondi, with woodland and forest areas considered separately. Adapted from Table 1 of Recher *et al.* (1985).

	PLOT (WL)			
	1		2	
HISTORY	Logged, Grazed		Logged, Grazed	
STRUCTURE	Woodland	Dry, Open-Forest	Woodland	Dry, Open-Forest
AREA (ha)	5	5	4	6
% CANOPY TREE SPECIES				
<i>Eucalyptus dalrympleana</i>	4	2	11	27
<i>E. ovata</i>	8	9	0	0
<i>E. pauciflora</i>	29	7	56	1
<i>E. stellulata</i>	35	8	11	0
<i>E. radiata</i>	20	60	15	72
<i>E. viminalis</i>	1	14	<1	0
hybrids <i>pauciflora</i> X <i>radiata</i>	2	<1	6	0
CANOPY SPECIES DIVERSITY (H')	1.50	1.26	1.27	0.64
CANOPY HEIGHT (m) (x±se)	17±0.2	19±0.3	16±0.1	17±0.5
NUMBER SUBCANOPY SPECIES	7	7	2	2
NUMBER SHRUB SPECIES	2	7	5	2
% TOTAL FOLIAGE				
CANOPY	69	74	59	72
SUBCANOPY	20	17	27	18
SHRUB	10	5	12	9
GROUND VEGETATION	1	4	2	1

with starting times for transects alternated. Counts were conducted by H.F. Recher and J. Shields who alternated between plots. All birds seen and heard within 60 m to either side of the transect line were recorded, including birds flying overhead (e.g., raptors), if it was considered they were using the plot or its airspace to forage.

Foraging Behaviour

Foraging observations were recorded at monthly intervals during the non-breeding season; 25–29 March, 23–28 April, 27–29 May, and 23–28 July, 1980 using the procedures and terminology described in Recher *et al.* (1985). Briefly, for each bird encountered we recorded up to five consecutive foraging attempts or prey-attacks. For each attempt, we recorded the plot, day, and time of day, the foraging manoeuvre (e.g., glean, probe, hawk) used by the bird, the substrate on which the prey was located (e.g., foliage, ground, branch), the height of the prey above ground, the sex of the bird where that could be determined, and the plant species/genus or type (e.g., fern, grass, shrub) when neither the species nor genus was known on which the prey was located. A prey-attack was recorded regardless of whether or not it was successful; most prey were too small to be certain they were taken or not. Heights were estimated to the nearest meter above 3 meters and to the nearest 25/50 centimetres below 3 meters.

Data Analysis

Abundance Data

The four counts for each transect were averaged as an estimate of species' abundances for each transect during July.

Foraging Data

The foraging data collected are not independent. However, Recher and Gebski (1989) showed there were no significant differences between the 1st and 2nd and subsequent observations, and in the analysis of the data all observations are treated as single observations.

Following Recher *et al.* (1985) and Holmes and Recher (1986), foraging observations from WLs 1 and 2 were combined and the plots treated as a single unit. Only species with 50 or more observations were used in analyses. Foraging substrates and foraging manoeuvres are presented as percents of total foraging observations; number of foraging observations is given in Table 2. Following Recher *et al.* (1985) foraging heights were grouped by vegetation layers: ground and debris, including logs, (0–20 cm), forbs and shrubs (>0.2 – 4.0 m), subcanopy and small trees (4.1 – 10.0 m), and canopy (>10.0 m).

Some substrates and foraging manoeuvres recorded in the field were combined to improve sample sizes for analysis. The substrates combined are large and small branches, including those with and without loose bark, as 'branches'; foliage and twigs, along with dead foliage, as 'foliage'; feeding on eucalypt capsules is described as 'seed'; and, tree trunks with and without loose bark are combined as 'trunk'. Dead and live substrates were combined in their respective categories. Among foraging

manoeuvres, probe and glean are combined as 'glean', and hover/hawk and hawk as 'hawk', as it was not always possible to separate these manoeuvres in the field.

Differences in the use of eucalypt species as foraging substrates were tested by Chi square.

Multivariate Analyses

Cluster analysis (CA) and Principal Components Analysis (PCA) were used to describe foraging guilds and distinguish between species. The foraging data matrix comprised 23 species (rows) by 14 foraging manoeuvre/substrate categories (columns) (Appendix A). Foraging relationships among birds can be described using cluster analysis whereby bird species are grouped according to the similarity the manoeuvre/substrates each uses. The groups can then be used to define guilds, with a guild being a cluster of species using similar food resources (Root 1967; Holmes and Recher 1986; Korňan *et al.* 2013).

For PCA, manoeuvre/substrate frequencies were log-transformed to reduce skewness and then standardized to bring the means to 0 and variances to 1.0. This weights all categories equally. The percent of manoeuvre/substrate observations were used in CA for the reason that transformed data yielded clusters that were difficult to interpret. For both CA and PCA the data were tested incorporating species weight and foraging height distributions. In neither case were the results more informative and only those analyses using the manoeuvre/substrate foraging frequencies in Appendix A are presented.

As neither CA nor PCA are statistical procedures to which probabilities can be applied, I selected results which accounted for the highest levels of variance and which seemed to best describe the relationships among species.

All statistical analyses were done using the PAST statistical package available from http://palaeoelectronica.org/2001_1/past/issue1_01.htm (Hammer *et al.* 2001, Hammer and Harper 2006).

Results

Species Abundances

During the non-breeding season (March–July), 50 species of birds were recorded during censuses on the two plots; 45 on WL 1 and 36 on WL2. Twenty-nine species were recorded during July counts, with 27 on WL1 and 20 on WL2 (Table 2). Species and scientific names are given in Table 2. Orange-winged Sittella was present on WL 1, but not recorded during counts. Birds were more abundant on WL1 than on WL2, with similar numbers of species and individuals on the forest transects (Table 2). The woodland transect on WL 1 had the greatest number of individuals and species, while that on WL 2 had the fewest (Table 2). Cluster analysis (Bray-Curtis) using the mean number of individuals recorded during the July counts grouped the two forest transects with a similarity of 0.72. The woodland transect on WL 1 had a similarity of 0.64 with the two forest transects. The woodland transect on WL 2 was separated from the other transects with a similarity of 0.53, that is, it was the most different of the four transects.

Table 2. Abundances of bird species observed on Bondi plots, WLs 1 and 2, in winter 1980. Abundances are the mean number of individuals recorded on parallel woodland and forest transects on each plot during four x 2 hour counts conducted on consecutive mornings, 23-26 July. Each transect was ~ 5ha in area.

Species***	No.* Obs	Wgt**(gm)	Abundance			
			WL 1		WL 2	
			Woodland	Forest	Woodland	Forest
Herbivores						
Crimson Rosella (<i>Platycercus elegans</i>)	585	116	1.75	1	1	0
Gang-gang Cockatoo (<i>Callocephalon fimbriatum</i>)	105	219	0	0	2	0.5
Insect-eaters						
Australian Raven (<i>Corvus coronoides</i>)	0	557†	0.5	0	0	0
Brown Thornbill (<i>Acanthiza pusilla</i>)	543	7	6	6.5	2.3	4.5
Buff-rumped Thornbill (<i>A. reguloides</i>)	339	8	14.8	0	0	0
Eastern Shrike-tit (<i>Falcunculus frontatus</i>)	97	29	1	0	0.5	0
Eastern Yellow Robin (<i>Eopsaltria australis</i>)	218	20	3.5	1.8	1.5	3
Flame Robin (<i>Petroica phoenicea</i>)	164	13	0	0	1	1
Golden Whistler (<i>Pachycephala pectoralis</i>)	0	25	0.3	0.3	0	0.3
Grey Currawong (<i>Strepera versicolor</i>)	60	168†	0	0	0	1
Grey Fantail (<i>Rhipidura fuliginosa</i>)	270	9	0.8	0.8	0	0.8
Grey Shrike-thrush (<i>Colluricincla harmonica</i>)	64	76	1.3	1.5	1.3	1.5
Ground (Bassian) Thrush (<i>Zoothera lunulata</i>) (<i>Z. dauma</i>)	280	106	3.3	1.5	3.3	1.5
Laughing Kookaburra (<i>Dacelo novaeguineae</i>)	0	340†	0.5	2.3	1.8	2
Olive Whistler (<i>P. olivacea</i>)	0	40†	0	0.3	0	0
Orange-winged Sittella (<i>Neositta (Daphoenositta) chrysoptera</i>)	75	12	0	0	0	0
Red-browed Treecreeper (<i>Climacteris erythrops</i>)	332	23	0.8	1	0.5	1.8
Scarlet Robin (<i>Petroica multicolor</i>)	71	13	1.5	0	0	0
Spotted Pardalote (<i>Pardalotus punctatus</i>)	0	8	0.3	0	0	0
Striated Pardalote (<i>P. striatus</i>)	28	12	1	0.5	0	0.3
Striated Thornbill (<i>A. lineata</i>)	1048	7	16.3	17.3	8.5	15.3
Superb Blue (Fairy) Wren (<i>Malurus cyaneus</i>)	1099	10	8	4	3	5.5
White-browed Scrubwren (<i>Sericornis frontalis</i>)	166	13	1	0.8	0	0.8
White-throated Treecreeper (<i>Cormobates leucophaea</i>)	342	22	1.8	0.8	1.3	2.8
White-winged Chough (<i>Corax melanorhamphos</i>)	195	379	0	0	0	0
Yellow-rumped Thornbill (<i>A. chrysorrhoa</i>)	55	9	1.5	0	0	0
NECTAR-FEEDERS						
Brown-headed Honeyeater (<i>Melithreptus brevirostris</i>)	88	15	3.8	0	0.3	1
Crescent Honeyeater (<i>Phylidonyris pyrrhopterus</i>)	20	16	1	1.5	0.8	0.5
White-eared Honeyeater (<i>Meliphaga (Lichenostomus) lecotis</i>)	212	25	5.5	3.3	1.8	1
White-naped Honeyeater (<i>Melithriptus lunatus</i>)	561	15	7.8	5.5	0.3	1.5
Yellow-faced honeyeater (<i>Meliphaga (Lichenostomus) chrysops</i>)	1	17	0.3	0	0	0
Number individuals (x±sd)			84±13	51±12	29±11	52±18
Number species (x±sd)			17±4	14±3	11±2	12±5
Total species			25	19	17	20

*Number of foraging manoeuvres or prey-attacks recorded in March, May, and July 1980. Only species with 50 or more observations are considered in the analyses.

**Weights are means obtained from birds mist-netted on the plots; †taken from the Birds in Backyards web site >www.birdsinbackyards.net/species<.

***Scientific and English names follow Recher et al. (1985) and CSIRO (1969); *Zoothera dauma* has been validly revised as *Z. lunulata* (Christidis and Boles 2008). Changes and revisions of scientific and/or English names for Grey Fantail, Orange-winged Sittella, and Scarlet Robin are considered to be without valid scientific reason and are not accepted. Alternative names are in parentheses. For consistency with previous papers based on this research, White-eared Honeyeater and Yellow-faced Honeyeater, which are presently placed in the genus *Lichenostomus* by Christidis and Boles (2008), are retained in the genus *Meliphaga* pending a full revision of the family Meliphagidae.

Breeding migrants remained abundant on the plots through March, but most had departed by the end of May (unpubl. counts). Those that remained through July were Grey Fantail, Flame Robin, Scarlet Robin, Spotted and Striated Pardalotes, and Yellow-faced Honeyeater. Compared with their abundances on the plots during the breeding season (see Table 2 in Recher *et al.* 1985), all were present only in small numbers, mostly one or two individuals (Table 2). Although numbers differed between monthly counts, all other species can be considered breeding residents, with numbers during July similar to those found during the breeding season.

Foraging Patterns

Sufficient data for analysis of winter (non-breeding) foraging patterns were obtained for 23 species of birds.

Foraging Substrates and Diet

Ten species foraged predominantly on the ground (Table 3). Eight of these took more than 75% of their food from the ground, including from coarse woody debris, litter, logs, and ground vegetation. In addition to ground-foraging, Scarlet and Flame Robins frequently took insects from the air (hawked), while Buff-rumped Thornbill also foraged in shrubs and the lower canopy where most prey was taken from bark (Tables 3, 7). Grey Shrike-thrush foraged about equally on the ground and in the canopy and sub-canopy where they took most prey from bark (Table 3). Crimson Rosella foraged on the ground (Table 7), but was grouped in Table 3 as a 'seed-eater', as their foraging on the ground was feeding on the seed heads of grasses and forbs.

Table 3. Substrates of food taken by forest and woodland birds at Bondi during winter (March-July) 1980. Numbers are percent of prey-attacks recorded. See Table 2 for scientific names.

Substrates	Ground	Bark			Foliage	Air	Nectar	Seed
		Trunk	Branch	Hanging bark				
Ground-foragers								
Ground Thrush	100							
Yellow-rumped Thornbill	100							
White-winged Chough	100							
Superb Blue Wren	98.6				1.4			
White-browed Scrubwren	89.8		3		6.6	0.6		
Eastern Yellow Robin	86.7	3.7	0.5		3.7	5.4		
Scarlet Robin	85.9				2.8	11.3		
Buff-rumped Thornbill	77.3	2.9	16.2		2.1	1.5		
Grey Shrike-thrush	53.1	7.8	15.6	11	12.5			
Flame Robin	48.4	6.3			2.5	42.8		
Bark-foragers								
Tree trunks								
White-throated Treecreeper		73.7	22.5	3.8				
Branches								
Orange-winged Sittella		26.7	73.3					
White-eared Honeyeater		9.4	63.2	2.4	8	16	1	
Eastern Shrike-tit		16.5	58.8	20.6	4.1			
Brown-headed Honeyeater			58.3		8.3		33.4	
White-naped Honeyeater		5	53.4	0.9	25	1.6	14.1	
Red-browed Treecreeper		50.6	47.6	1.8				
Hanging bark								
Grey Currawong			16.7	83.3				
Bark & Foliage-foragers								
Brown Thornbill	10.3	7.2	33.3	1.3	44.5	1.7	1.7	
Striated Thornbill		1.5	20	0.5	76	0.8	1.2	
Aerial-foragers								
Grey Fantail	2.2				11.1	86.7		
Seed-eaters								
Gang-gang Cockatoo								100
Crimson Rosella		0.9	46.1		3.4		0.9	48.7

Bark-foragers were the next most diverse group of species, with eight species taking more than 50 % of their food from tree trunks, branches (large and small), and hanging bark (on trunks and branches) (Table 3). White-throated and Red-browed Treecreepers foraged exclusively on bark, with White-throated Treecreeper feeding more on trunks and Red-browed Treecreeper more on branches (Table 3). Both species favoured substrates with loose or decorticating bark, which they gleaned and probed, but rarely prised or flaked (<1% of observations). Orange-winged Sittella foraged most often on branches and, although it was not recorded as part of field observations during winter, selected dead over live substrates, as they did during summer (pers obs.; Recher and Holmes 1985). White-eared and Brown-headed Honeyeaters probed loose bark on branches, while Brown-headed and White-naped Honeyeaters took nectar and fed frequently from foliage (Table 3). Eastern Shrike-tit and Grey Currawong primarily probed loose and hanging bark for arthropods.

Two species, Brown and Striated Thornbills, were grouped as bark and foliage foragers (Table 3). Brown Thornbill took insects about equally from bark (most often small branches)

and foliage, but also foraged on the ground taking insects from litter and woody debris. More than 75% of foraging by Striated Thornbill was on foliage, with small branches the next most frequently used substrate (Table 3).

Grey Fantail was the only predominantly aerial forager (Table 3), although they were observed to snatch prey from foliage and gleaned insects from the ground. Gang-gang Cockatoo and Crimson Rosella were grouped as seed-eaters. Gang-gang Cockatoos foraged exclusively on eucalypt capsules. Crimson Rosella took seeds from eucalypt capsules, but took 30% of seed from the ground and low vegetation (Table 7).

Foraging Manoeuvres

Gleaning was the most frequently used foraging behaviour, with 15 species using glean as their principal (>50%) prey-attack manoeuvre (Table 4). Five species foraged mostly by probing, with probing also a frequent behaviour of White-throated Treecreeper and White-naped Honeyeater. Probers took most prey from under and among loose bark, including decorticated bark hanging from branches and trunks. Probing included taking nectar.

Table 4. Percent of foraging manoeuvres used by forest and woodland birds at Bondi during the winter (March-July) of 1980. See Table 2 for scientific names.

	Pounce	Probe	Glean	Hang/Glean	Hover	Snatch	Hawk
Pouncers							
Eastern Yellow Robin	89		0.9		0.5	4.1	5.5
Scarlet Robin	85.9					2.8	11.3
Probers							
Eastern Shrike-tit		85.6	13.4			1	
Grey Currawong		75	25				
Red-browed Treecreeper		67.2	32.8				
Brown-headed Honeyeater		58.3	40				
White-eared Honeyeater		50.5	31.1		1.9	0.5	1.6
Gleaners							
Yellow-rumped Thornbill			100				
White-winged Chough			100				
Crimson Rosella			100				
Gang-gang Cockatoo			100				
Red Wattlebird			100				
Ground Thrush		0.4	99.6				
White-browed Scrubwren			98.8			0.6	0.6
Superb Blue Wren			98.6				1.4
Buff-rumped Thornbill			98.5				1.5
Orange-winged Sittella		4	96				
Brown Thornbill		3.9	75	1.6	7.7	10.1	1.7
White-throated Treecreeper		30.1	69.6			0.3	
Striated Thornbill		4.3	65.7	19.7	7.1	2.4	0.8
Grey Shrike-thrush		14.1	64			21.9	
White-naped Honeyeater		43.7	54.5			0.2	1.6
Hawkers							
Grey Fantail			2.2			11.1	86.7
Flame Robin	37.7		14.5		1.2	3.8	42.8

Hang-gleaning distinguished the foraging behaviour of Striated Thornbill and was used to extract insect larvae from among leaves that had been bound together by the larvae. Striated and Brown Thornbills were the only species to frequently hover (Table 4). Two species, Eastern Yellow and Scarlet Robins were pouncers (to ground and tree trunks). Pouncing was also a common behaviour of Flame Robin, which also hawked insects from the air (Table 4). Grey Fantail foraged mainly by hawking and snatching. Snatch was a frequent behaviour of Grey Shrike-thrush, while Scarlet Robin and White-eared Honeyeater also hawked (Table 4).

Use of Plant Species

Few plants flowered during the winter, with a total of 148 observations of nectar-feeding for eight species of birds: Brown Thornbill (9), Brown-headed Honeyeater (20), Crescent Honeyeater (10), Crimson Rosella (5), Red Wattlebird (10), Striated Thornbill (13), White-eared Honeyeater (2), and White-naped Honeyeater (79). Of these, 135 were of birds taking nectar from *E. dalrympleana* and four from *E. stellulata* (White-eared and White-naped Honeyeaters, 2 each). With the limited sample size, nectar-foraging was deleted from analyses of the use of plant species. After deleting nectar-feeding, there were sufficient data to analyse the use of plant species by 11 species of birds (Table 5).

Birds were recorded foraging on 13 species of plants: seven were eucalypts, including a hybrid between *E. radiata* and *E. pauciflora*, three were wattles (*Acacia terminalis*, *A. melanoxylon*, and *A. mearnsii*), and three were shrubs (*Daviesia* sp., *Persoonia* sp., and Blackthorn *Bursaria spinosa*). Ninety-six percent of the observations of birds taking food from vegetation were of birds feeding on eucalypts. Three percent were on wattles and one percent

on other genera. Brown Thornbills used the greatest variety of plants, foraging on all species of plants for which there were foraging observations. In addition to foraging on eucalypts, Striated Thornbills and Orange-winged Sittellas also foraged on wattles (<5% of observations), but not on any other genera.

Of the observations on eucalypts, 76% were on forest eucalypts (*E. radiata*, *E. dalrympleana*, and *E. viminalis*) and 24% on woodland eucalypts (*E. ovata*, *E. stellulata*, and *E. pauciflora*). There were significant differences in amounts of foraging recorded on the species of eucalypts proportional to their abundances, with higher proportions on *E. radiata*, *E. dalrympleana*, and *E. ovata* and less on *E. stellulata* and *E. pauciflora* than expected ($\chi^2_6 = 136.31$, $p < 0.001$) (Table 6). Among the forest eucalypts, significantly more foraging was recorded on *E. radiata* than on *E. dalrympleana* ($\chi^2_2 = 10.944$, $p = 0.004$). Foraging on *E. viminalis* was recorded in about the same proportion as the number of trees on the plots. Among woodland eucalypts, there was significantly more foraging on *E. stellulata* and *E. ovata* than on *E. pauciflora* ($\chi^2_3 = 50.996$, $p < 0.001$). Foraging on *E. radiata*/*E. pauciflora* hybrids was about the same as the proportion of hybrids on the plots, with the exception that Gang-gang Cockatoos foraged preferentially on the capsules of *E. radiata*/*E. pauciflora* hybrids (Table 5).

Cluster and principal components analyses segregated species according to the plants on which they foraged for foods other than nectar. After deleting Crimson Rosella and Gang-gang Cockatoo as seed eaters, cluster analysis identified two groups of birds: Brown and Striated Thornbills, Eastern Shrike-tit, and Orange Winged Sittella formed a cluster associated with foraging on *E. radiata*; Red-browed and White-throated Treecreepers along with White-eared and White-naped Honeyeaters formed a second cluster associated with foraging on *E. dalrympleana*,

Table 5. Percent use of plant species for non-nectar foraging by woodland birds during winter, 1980. Other includes *Acacia* spp. and *Bursaria spinosa*. A number of *Eucalyptus radiata*/*pauciflora* hybrids occurred on VL 1 and were distinguished by the size and aroma of their capsules. All observations were by HFR, with species having < 50 observations of taking food from plants deleted. Species are ranked according to the frequency of foraging on *E. radiata*.

	No. Obs	<i>Eucalyptus</i>							
		Forest <i>Eucalyptus</i>				Woodland <i>Eucalyptus</i>			
		<i>radiata</i>	<i>dalrympleana</i>	<i>viminalis</i>	<i>stellulata</i>	<i>radiata</i> x <i>pauciflora</i>	<i>pauciflora</i>	<i>ovata</i>	other
Crimson Rosella	420	94	1.2				4.8		
Orange-winged Sittella	75	93.3							6.7
Eastern Shrike-tit	112	73.2	6.2		7.1	8.9	4.5		
Striated Thornbill	1040	70.8	8.3	2.7	4.8	0.1	5.4	6.0	2.0
White-throated Treecreeper	343	58.0	5.5	2.9	15.5	2.9	10.8	4.4	
Red-browed Treecreeper	332	53.9	6.3		1.5		20.2	18.1	
White-eared Honeyeater	178	47.8	9.6	14.0	7.3		1.7	19.7	
Brown Thornbill	464	43.8	2.8	2.2	13.8		9.9	1.1	26.5
Buff-rumped Thornbill	72	41.7			51.4			6.9	
White-naped Honeyeater	443	38.8	17.4	9.0	1.1	1.1	6.5	26.0	
Gang-gang Cockatoo	105	19.0		28.6		38.1	14.3		

Table 6. Number and percent of *Eucalyptus* trees sampled during vegetation surveys on WLs 1 and 2, with the number and percent of foraging observations for all birds foraging for food other than nectar on eucalypts during the winter of 1980. Only bird species with > 50 observations were included. The percent composition of eucalypt species was adapted from Table 1 of Recher *et al.* (1985).

	Forest <i>Eucalyptus</i> species				Woodland <i>Eucalyptus</i> species		
	<i>radiata</i>	<i>dalrympleana</i>	<i>viminalis</i>	<i>stellulata</i>	<i>radiata</i> x <i>pauciflora</i>	<i>pauciflora</i>	<i>ovata</i>
No. Trees sampled	167	44	15	46	8	93	17
No. Foraging obs.	2171	322	143	237	66	278	297
% Trees	42.8	11.3	3.8	11.8	2.1	23.8	4.4
% Foraging	61.8	9.2	4.1	6.7	1.9	7.9	8.5

E. viminalis, and *E. ovata*. Within their respective clusters, Brown Thornbill was separated from other species by its higher frequency of foraging on *E. stellulata* and *E. pauciflora*, while White-throated Treecreeper foraged more frequently on *E. stellulata* than Red-browed Treecreepers. Red-browed Treecreepers foraged more on *E. pauciflora* and *E. ovata*, smooth-barked gums with abundant loose bark, than White-throated Treecreeper (Table 5). Buff-rumped Thornbill was separated from other species by its higher frequency of foraging on *E. stellulata*, with Gang-gang Cockatoo separated by its frequent use of *E. radiata*/*E. pauciflora* hybrids. Crimson Rosella clustered with species that foraged most frequently on *E. radiata*. Including non-eucalypts in the analyses added little information to the results, making little difference to the association of Brown Thornbill with other species, despite its frequent use of non-eucalypts when foraging (Table 5).

In the principal components analysis depicted in Figure 1, which considers only non-nectar foraging on eucalypts, Buff-rumped Thornbill was excluded as a ground-forager. The first two axes accounted for 84.8% of the total variance, with axis I accounting for 61.8% and axis II 23%. Axis I segregated species foraging on *E. dalrympleana* and *E. ovata* (positive values) from those foraging on *E. radiata* (negative values). Axis II segregated *E. radiata* (negative values) from other eucalypts (positive values). Buff-rumped Thornbills foraging on eucalypts foraged primarily on *E. stellulata* (51% of observations) and *E. radiata* (42%). With Buff-rumped Thornbill included, the first two axes accounted for 76% of the total variance.

Foraging Heights

Four species of birds foraged primarily in the canopy, with six others foraging in the subcanopy and shrub layers, as well as in the canopy (Table 7). Of these, the Crimson Rosella foraged extensively (30% of observations) on the ground. Four species foraged mainly in the subcanopy and shrub layers, with the Flame Robin also foraging on the ground (47%). The remaining nine species were classed as ground foragers, although four species, Superb Blue Wren, Scarlet Robin, White-browed Scrubwren, and Buff-rumped Thornbill, foraged frequently in the shrub layer. Buff-rumped Thornbills and Grey Shrike-thrush also foraged in the subcanopy, and the shrike-thrush frequently foraged in the canopy (30%) (Table 7).

Other than ground foragers, all species foraged over a wide height range as shown by the large standard deviations in mean foraging heights (Table 7). Five species foraged

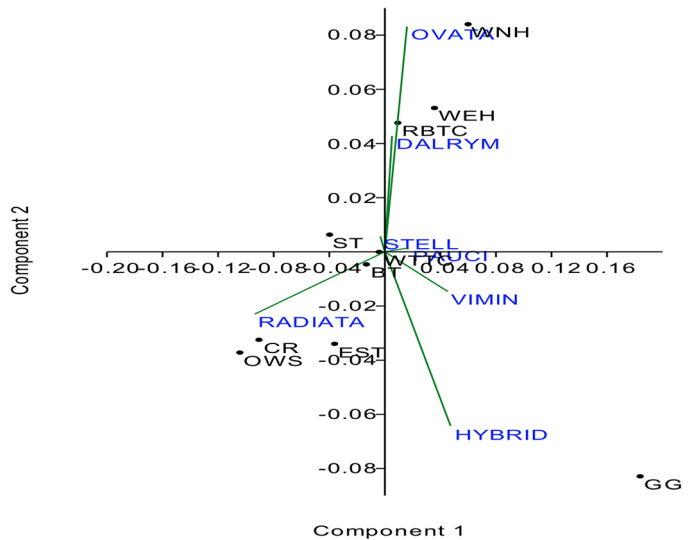


Figure 1. Projection of bird and eucalypt species along the first two principal component axes based on non-nectar foraging observations on eucalypts on WLs 1 and 2 combined, during winter, 1980. In this figure, Buff-rumped Thornbill has been excluded from the analysis as it foraged primarily on the ground. Otherwise, it was separated from the other species by its high frequency of foraging on *Eucalyptus stellulata*. The first two axes respectively account for 61.8 and 23% of total variance. Hybrids were identified as crosses between Snow Gum *E. pauciflora* and Narrow-leaved Peppermint *E. radiata*. Eucalypt species are *E. ovata*, *E. dalrympleana*, *E. stellulata*, *E. pauciflora*, *E. viminalis*, and *E. radiata*. Bird species are White-naped Honeyeater (WNH), White-eared Honeyeater (WEH), Red-browed Treecreeper (RBTC), White-throated Treecreeper (WTT), Crimson Rosella (CR), Orange-winged Sittella (OWS), Eastern Shrike-tit (EST), and Gang-gang Cockatoo (GG).

from the ground into the canopy, with seven others foraging from the shrub layer to the canopy.

Foraging Guilds

The foraging guild structure of the winter bird community was explored using cluster and principal components analyses based on the 14 manoeuvre/substrate foraging categories in Appendix A. As previously indicated, including body weight, mean foraging height, foraging height distribution, and use of plant species complicated the models and were not used in the analyses presented here.

Table 7. Foraging height distribution of forest and woodland birds on WLs 1 and 2 combined, at Bondi during winter (March – July) of 1980 expressed as percent of foraging observations by vegetation layer, with mean and standard deviation of foraging height.

Height range (m)	Vegetation layer				Foraging height
	Ground	Shrub	Subcanopy	Canopy	
	0 - 0.1	> 0.1 - 4.0	4.1 - 10.0	> 10.0	
Canopy					
Gang-gang Cockatoo				100	19.6±6.3
Brown-headed Honeyeater				100	19±3.6
Grey Currawong				100	14.1±8.5
White-naped Honeyeater		7	19	74	15.3±3.6
Subcanopy/canopy					
White-eared Honeyeater		7	26	67	15.3±6.6
Striated Thornbill		11	24	64	13.2±7
Crimson Rosella	30	3	9	58	13.9±6.4
Grey Fantail	7	28	13	52	10.9±8.5
Eastern Shrike-tit		4	45	51	11.6±5.6
Red-browed Treecreeper		29	21	50	10.5±6.5
Shrub/subcanopy					
Orange-winged Sittella		13	47	40	10.3±6.4
White-throated Treecreeper		40	32	28	8.1±7.4
Brown Thornbill	7	65	20	7	6.2±6.3
Flame Robin	47	29	18	5	2.6±4
Ground					
White-winged Chough	100				0
Yellow-rumped Thornbill	100				0
Ground Thrush	100				0
Eastern Yellow Robin	92	5	3		0.3±1.2
Superb Blue Wren	87	13			0.04±0.1
Scarlet Robin	84	16			0.3±0.8
White-browed Scrubwren	79	21			0.1±0.1
Buff-rumped Thornbill	75	12	13		1.3±2.8
Grey Shrike-thrush	51	5	14	30	6±7.7

Cluster Analysis

The cluster analysis separated six groups of species, which can be identified as guilds based on foraging similarities (Figure 2). The six guilds are characterized in the following ways: Guild I consists of seven species that foraged predominantly on the ground (> 50% of foraging observations). Grey Shrike-thrush, Buff-rumped Thornbill, and White-browed Scrubwren are separated within this group as they also foraged above ground on bark and foliage substrates, with the shrike-thrush foraging into the canopy. All species within this guild were predominantly gleaners (75-100%), with the shrike-thrush also snatching prey (22%). Guild II contains seven species that foraged predominantly (58-100%) on bark substrates. Both treecreepers and the Orange-winged Sittella foraged exclusively on bark substrates, with the two treecreepers differing in the frequency of trunk and branch foraging. Sittellas foraged most often (73%) on branches. In addition,

the remaining four species took prey from foliage, with Brown-headed and White-naped Honeyeaters also taking nectar. Gleaning was the predominant foraging behaviour within this group, but much of the behaviour of all species involved probing among and under loose bark on branches and trunks. Although separated in the analysis, Grey Currawong foraged exclusively on bark and was considered part of the bark-foraging guild. More than 80% of its prey was taken by probing hanging bark thereby separating it from other bark-foragers. Guild III consists of Brown and Striated Thornbills. Both foraged frequently on bark substrates (42% and 22% respectively), but also took prey from foliage (46% and 76% respectively) grouping them as bark/foliage foragers. Striated Thornbill hang-gleaned, a behaviour rarely used by other thornbills. Guild IV is a seed-eating guild consisting of Gang-gang Cockatoo and Crimson Rosella. Crimson Rosella also gleaned the loose bark of branches (46%), where it appeared to be taking

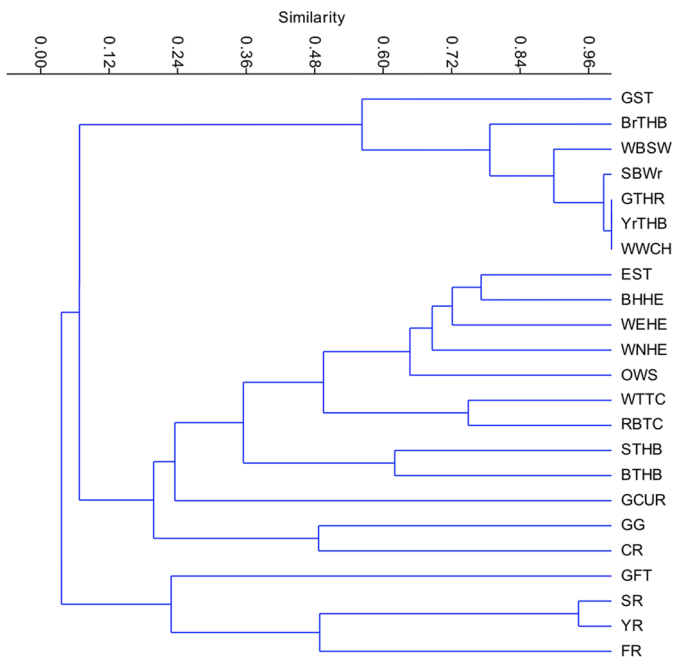


Figure 2. Cluster diagram of foraging similarity of 23 species of birds on WLs 1 and 2 combined, at Bondi during Winter, 1980. Six guilds with a similarity > 0.48 are identified, with Grey Currawong an outlier. The guilds are discussed in the text. Analysis was done using the Bray-Curtis Similarity Measure (Coph. Corr. = 0.9325) in the PAST statistical package and based on the 14 manoeuvre/substrate categories in Appendix A. Guilds and bird species are: I. Grey Shrike-thrush (GST), Buff-rumped Thornbill (BrTHB), White-browed Scrubwren (WBSW), Superb Blue Wren (SBWr), Ground Thrush (GT), Yellow-rumped Thornbill (YrTHB), White-winged Chough (WWCH); II. Eastern Shrike-tit (EST), Brown-headed Honeyeater (BHHE), White-eared Honeyeater (WEHE), White-naped Honeyeater (WNHE), Orange-winged Sittella (OWS), White-throated Treecreeper (WTTC), Red-browed Treecreeper (RBTC); III. Striated Thornbill (STHB), Brown Thornbill (BTHB); IV. Gang-gang Cockatoo (GG), Crimson Rosella (CR); V. Grey Fantail (GFT); and, VI. Scarlet Robin (SR), Eastern Yellow Robin (YR), Flame Robin (FR). Grey Currawong (GCUR) is best placed with the bark-foragers in guild II.

scale insects. Gang-gang Cockatoo fed exclusively on the ripening capsules of eucalypts. Guild V is an aerial foraging or hawking guild consisting solely of the Grey Fantail. Guild VI comprises three species that foraged predominantly (>80%) by ground pouncing and hawking, with Eastern Yellow and Scarlet Robins taking most (>85%) prey by pouncing and the Flame Robin hawking (43%) and pouncing (38%) in about equal proportions.

Principal Components Analysis

Principal component analysis sorted species into broadly the same guilds as cluster analysis: ground-foragers, bark and foliage foragers, and pouncers and hawkers (Figure 3). As a seed-eater, the Crimson Rosella was grouped with bark and foliage foragers, with the Gang-gang Cockatoo separate (Figure 3). The first two axes (components) accounted for 41 and 21% of community variance respectively, with the first four axes accounting

for 74% of the variance. Axis I segregated ground, bark, and foliage foragers (positive values) from aerial foragers and pouncers (negative values). Axis II segregated above ground foragers (positive values) from ground and low vegetation foragers (negative values). Axis III (12% of variance) segregated seed eaters (negative value) from others. Axis IV (8%) segregated pouncers (negative values) from hawkers (positive values). Axes V and VI (7 and 6% respectively) segregated gleaning/probing tree trunks (negative) from gleaning /probing hanging bark (positive), and gleaning/probing hanging bark and gleaning/probing trunks (negative) from gleaning branches and foliage (positive). Thus, species were sorted into and within guilds on the basis of foraging substrates and the manoeuvres used to take food.

Discussion

The winter bird community at Bondi was a subset of the summer community; only Olive Whistler *Pachycephala olivacea* occurred on the plots in winter, but not during the breeding season. During December (Summer) 1980, 38 species (176 individuals) were present on WL 1, with 35 species (178 individuals) on WL 2 (Table 2, Recher *et al.* 1985). This compares with 26 species (135 individuals) on WL 1 and 22 species (81 individuals) on WL 2 during winter (*op. cit.*). The numbers of migratory species on the plots declined sharply from December 1979 to May 1980, when few migrants remained on the plots (Figure 2 in Recher and Holmes 1985; Recher *et al.* 1983a). Abundances of resident species remained stable or increased during winter (*op. cit.*), although increases could be an artefact of greater detectability during the non-breeding season (Emlen 1971, Ralph 1981, Best and Peterson 1985, Recher 1989, Poprach *et al.* 2015). As Hugh Ford (*in litt.*) noted, it is possible that migrants from other areas replaced resident individuals that in turn migrated.

Holmes and Recher (1986) recognized nine foraging guilds among 41 species of birds present on the Bondi plots during the summer of 1980/81 compared with the six guilds among 23 species during winter 1980 (Figure 1). The analysis of Holmes and Recher (1986) included foraging observations from a third plot (WL 3) that was unlogged, not grazed, and dominated by tall, moist sclerophyll forest (see Recher *et al.* 1985 for details). As species present on WL 3, but absent from the other plots, clustered within the same guilds as species from WLs 1 and 2, it can be taken that there were nine recognizable guilds during summer on WLs 1 and 2 compared with the six foraging guilds present in winter (Figure 1). The analysis of Holmes and Recher (1986) included body weight with four guilds separated by size; large and small ground foragers, and large and small aerial foragers. By ignoring body weight the number of guilds is reduced to seven, which is the same as obtained by Korňan *et al.* (2013) using different statistical procedures, but the same data, if body weight is also excluded from their analysis. The guilds identified by Korňan *et al.* (2013) are the same as reported by Holmes and Recher (1986), but the species composition of the guilds identified differed.

The seven guilds as recognized by Korňan *et al.* (2013) are: I. Nectar-feeders (3 species); II. Ground-gleaners (10); III.

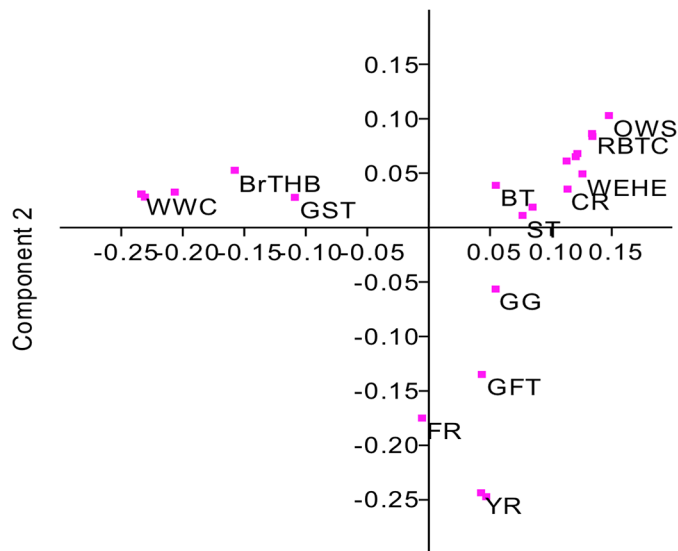


Figure 3. Principal components plot of 23 bird species on WLCs 1 and 2 combined, during the winter of 1980. The analysis was done using the 14 manoeuvre/substrate categories in Appendix A to define each species foraging characteristics. In this figure, only indicator species are labelled; White-winged Chough (WWC), Buff-rumped Thornbill (BrTHB), Grey Shrike-thrush (GST), Brown Thornbill (BT), Striated Thornbill (ST), Crimson Rosella (CR), White-eared Honeyeater (WEHE), Red-browed Treecreeper (RBTC), Orange-winged Sittella (OWS), Gang-gang Cockatoo (GG), Grey Fantail (GFT), Flame Robin (FR), Eastern Yellow Robin (YR). Component 1 separates aerial foraging and ground pouncing species (GFT, FR, YR) from bark (OWS, RBTC, WEHE, CR) and foliage foragers (BT, ST). Component 2 separates ground foragers (WWC, BrTHB, GST) from others. Seed eaters (GG, CR) overlap the bark and foliage foraging guilds.

Foliage, twig, small branch foragers (8); IV. Bark foragers (5); V. Aerial-foragers and snatchers (9); VI. Seed-eaters (2); and, VII. Ground-pouncers (4). Recher *et al.* (1985) used a flow chart to describe the foraging guilds for the summer bird community at Bondi. They included habitat, as well as body size, in sorting species into foraging guilds, with an initial separation of species by food type: nectar feeders (8 species), seed eaters (2), and insect-eaters (31). Insect-eaters were then separated into ground and above ground foragers, with subsequent separation into guilds based on body weight, habitat (woodland or forest), foraging manoeuvre, and foraging substrate. The broad guilds recognized among insect-eaters were ground foragers (13 species), including gleaners (9) and pouncers (4), bark foragers (5), including gleaners (3) and probers/prisers (2), and foliage gleaners (4) and snatchers (5), and aerial foragers (4), with further segregation by habitat and vegetation layer (canopy and shrub foragers).

Absent from, or poorly represented in, the winter community considered in this paper are the nectar-feeder and aerial-forager/snatcher guilds recognized in the guild analyses of Holmes and Recher (1986) and Korňan *et al.* (2013). The species forming these guilds in summer were either absent or present only in reduced numbers during winter. Of the 12 species forming these guilds in the analysis of Korňan *et al.* (2013), nine were not recorded

during the July 1980 census. Two other species, Fan-tailed Cuckoo *Cuculus pyrrhophanus* (ground-pouncing guild) and Silvereye *Zosterops lateralis* (foliage-gleaner) were also absent. Three foliage-gleaners, Yellow-faced Honeyeater, and Spotted and Striated Pardalotes, were present only in small numbers, as were Grey Fantail (aerial forager), and Scarlet and Flame Robins (ground pouncers). Differences between summer and winter in the number and abundance of species are correlated with the abundance of food resources (Recher *et al.* 1983a, 1985). Nectar, and ground, bark, foliage, and flying arthropods were most abundant during spring, summer, and autumn (late September – early May, and least abundant during winter (late May – early September) (Recher *et al.* 1983a). Similar seasonal changes in the abundance of canopy and bark arthropods in eastern and western Australia were reported by Recher *et al.* (1996) and Majer *et al.* (2003). Eucalypt seed capsules, although abundances differed seasonally among tree species, were available throughout the year (Recher *et al.* 1983a).

Birds respond to seasonal and annual differences in food resources by migration, local movement, and changes in their foraging behaviour (Cale 1994; Wilson and Recher 2001). At Bondi where winters are cold, food resources are less in winter than in spring and summer (Recher *et al.* 1983a). For this reason, many species, if not all individuals, migrate to coastal and/or more northerly habitats where it is warmer and food is abundant. Based on the species that migrate, food shortages were greatest for species dependent on relatively large prey, such as foliage snatchers, aerial foragers, and ground pouncers, with the exception of Eastern Yellow Robin, and foliage-gleaners dependent on energy rich carbohydrates (e.g., nectar, lerp), such as pardalotes and Silvereye. This leaves the question as to why other ground foragers and bark foragers, as well as Brown and Striated Thornbill remain abundant through winter. As ground gleaners and the thornbills, which are primarily foliage and bark gleaners, are searchers that take less active prey than birds that rely on pursuit to capture their food, their food supply may remain abundant or more accessible during winter, a point made by Hugh Ford (*in litt.*).

The procedures used to sample arthropod and nectar abundances are described in Recher *et al.* (1983a), but were affected by the abundances of arthropods and their level of activity (*pers obs*). Thus, although the sampled abundances and biomass of all categories of arthropods were least in winter (Figures 5 and 6 in Recher *et al.* 1983a), insects and spiders were available on bark and foliage throughout the year and were probably more abundant in winter than measured. Nectar, as measured by floral abundance, was limited in winter relative to other seasons and restricted to *E. stellulata* and *E. ovata* on WL 1, and *E. dalrympleana* on WL 2 (Figure 8 in Recher *et al.* 1983a). The scarcity of nectar during winter explains the reduced abundance of nectar-feeders on the plots. Richard Loyn (*in litt.*) points out that scarcity of nectar during winter is not a universal feature of forests and woodlands in southern Australia. The flowering of eucalypts and the spatial abundance of nectar varies significantly between years (*pers obs.*; Keast 1967; Paton 1985; McGoldrick

and Mac Nally 1998; Franklin and Noske 1999) and it is possible that the winter of 1980 was a poor year for nectar production on the two plots studied. The honeyeaters that remained on the plots (Brown-headed, White-eared, and White-naped Honeyeaters) foraged mainly by probing and gleaning bark, where they accessed arthropods and energy-rich carbohydrates in the form of honeydew (pers obs.), with the White-naped Honeyeater also gleaning lerp from foliage (pers obs.) Brown-headed and White-naped Honeyeaters also took nectar from *E. dalrympleana*, *E. stellulata*, and *E. ovata*. Hawking by White-eared and White-naped Honeyeaters occurred throughout the winter in the upper canopy of trees where the sun's warmth probably increased insect activity.

Ground-foragers remained abundant through winter, with some species increasing the amount of ground foraging (e.g., Buff-rumped Thornbill, Grey Shrike-thrush, Scarlet and Eastern Yellow Robins) and others decreasing (e.g., Flame Robin). Recher (1989) also reported an increase in ground-foraging by Buff-rumped Thornbill in autumn and winter relative to spring and summer, but was unable to explain it. The increase in ground-foraging by these species was accompanied by a decrease in the amount of foliage and aerial foraging suggesting that ground invertebrates were more accessible during winter than foliage and aerial arthropods. Ford *et al.* (1990) also suggested that increased ground foraging during winter by Australian passerines indicated food resources were relatively more abundant on the ground than other substrates during winter. In line with the decline in flying insects and aerial foragers, ground, bark, and foliage foragers took less aerial prey. The exceptions were the Flame Robin, which took more aerial prey and less ground prey, and the White-eared Honeyeater, which took more aerial prey and less from bark and foliage. Striated and Brown Thornbills foraged less on foliage and more on bark during winter suggesting a greater reduction in foliage arthropods during winter than of bark arthropods. Among seed-eaters, the Crimson Rosella took fewer seeds and did more bark foraging than in summer, which reflects its preference for foraging on the seed capsules of *E. radiata*, which were most abundant during summer (Recher *et al.* 1983a, 1985). Differences in the proportions of foraging manoeuvres among species between winter and summer are linked to the seasonal differences in substrate use, with fewer manoeuvres, such as hover, snatch, and hawk, associated with foliage and aerial foraging in winter and greater use of glean and probe, associated with bark foraging, behaviours.

It is difficult with the data available to explain differences in the selection of eucalypt species as foraging substrates. The exception to this is the preference shown by Gang-gang Cockatoo for the seed capsules of *E. pauciflora*/*E. radiata* hybrids. The hybrid's capsules were larger than those of *E. radiata*, but smaller than those of *E. pauciflora*. However, like *E. radiata* the hybrid's capsules were aromatic, smelling of peppermint. It is therefore possible that Gang-gang

Cockatoo preferred the more aromatic capsules of *E. radiata* to the less aromatic capsules of *E. pauciflora*, and the larger size of hybrid capsules made them particularly attractive. All seed set by hybrids on both plots was consumed by cockatoos, whereas some seed remained on *E. pauciflora* and *E. radiata* until shed (pers obs.).

Abbott and Van Heurck (1985) found selection among foliage-foraging insectivores for different tree species in Western Australian Jarrah *E. marginata* forest, which they predicted would be related to differences between tree species in the kinds of arthropods found on different species. Recher and Majer (1994) working in eastern Australia found species of Acanthid warblers selected between tree species according to the abundance of psyllid insects, with psyllid specialists, such as Weebill *Smicromis brevirostris* and Striated Thornbill, foraging preferentially on Narrow-leaved Ironbark *E. crebra*, which had the greatest abundance of psyllids. Other differences between species in the use of eucalypt species as foraging substrates can be attributed to habitat selection (e.g., woodland vs forest) and the type of bark characteristic of the different species of eucalypts (Recher *et al.* 1985). For example, during summer, Red-browed Treecreeper foraged more on gums and probed loose bark more frequently than White-throated Treecreeper, which foraged significantly more often on rough-barked eucalypts and was predominantly a gleaner (Recher *et al.* 1985). Red-browed Treecreepers also foraged more frequently in winter on gums with abundant loose bark.

Conservation Management

Although birds were affected by the seasonal changes of food abundances and entire guilds of species left the area for the winter, the Bondi woodlots retained a diverse and abundant avifauna. This is despite a long history of disturbance including logging, clearing, and grazing. The reason for the continued abundance and diversity of species through the winter can be explained by the variety of food resources available for birds; the complexity of foliage, bark, and ground substrates provided a wide range of foraging substrates over the entire vertical profile of the vegetation. Only aerial prey and nectar decreased in abundance during winter to the point that specialist foragers on those substrates could not be sustained, at least not in the numbers found during the warmer months of the year. Additional diversity was provided by the variety of tree and shrub species, as well as ground vegetation, each of which appeared to provide unique foraging opportunities for different species of birds. If there is a conservation and management lesson in these observations, it is that eucalypt forest and woodland birds rely on complexly structured vegetation communities in terms of both the physical and the biological environment. Some management actions, such as frequent, periodic burning, grazing by domestic stock, and logging, reduce the diversity of resources available to birds and lead to declines in species' abundances and species richness.

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APPENDIX A.

Percent utilization of 14 manoeuvre/substrate foraging categories for 23 bird species on two plots (WL 1 and WL 2) at Bondi, New South Wales during winter (May – July; the non-breeding season) used in cluster and principal components analyses.

	Glean Trunk	Glean Branch	Glean Hanging Bark	Glean Leaf	Hang-glean Leaf	Glean Ground	Eat Seed	Probe Nectar	Pounce Ground	Hawk	Snatch Leaf	Snatch Bark	Hover Bark	Hover Leaf
Brown-headed Honeyeater	5.7	53.4	17.0	0	0	0	0	22.7	0	0	1.1	0	0	0
Brown Thornbill	5.7	31.1	1.3	28.9	1.5	10.3	0	1.7	0	1.7	8.7	1.5	2.2	5.5
Buff-rumped Thornbill	2.9	16.2	0	2.1	0	77.3	0	0	0	1.5	0	0	0	0
Crimson Rosella	0.9	46.2	0	3.4	0	0	48.7	0.9	0	0	0	0	0	0
Eastern Shrike-tit	16.5	58.8	20.6	3.1	0	0	0	0	0	0	1.0	0	0	0
Eastern Yellow Robin	0	0	0	0	0	0.9	0	0	89.0	5.5	3.2	0.9	0	0.5
Flame Robin	0	0	0	0	0	14.0	0	0	36.6	41.5	3.7	3.0	1.2	0
Gang-gang Cockatoo	0	0	0	0	0	0	100.0	0	0	0	0	0	0	0
Grey Currawong	0	17.6	82.4	0	0	0	0	0	0	0	0	0	0	0
Grey Fantail	0	0.7	0	0	0	0.4	0	0	0	88.1	10.8	0	0	0
Grey Shrike-thrush	3.1	9.4	10.9	1.6	0	53.1	0	0	0	0	10.9	10.9	0	0
Ground Thrush	0	0	0	0	0	100.0	0	0	0	0	0	0	0	0
Orange-winged Sittella	26.7	73.3	0.0	0	0	0	0	0	0	0	0	0	0	0
Red-browed Treecreeper	50.6	47.6	1.8	0	0	0	0	0.0	0	0	0	0	0	0
Scarlet Robin	0	0	0	0	0	0	0	0	85.9	11.3	2.8	0	0	0
Striated Thornbill	1.5	19.5	0.6	47.2	19.8	0	0	1.2	0	0.8	2.1	0.3	0.2	6.9
Superb Blue Wren	0	0	0	0	0	98.6	0	0	0	1.4	0	0	0	0
White-browed Scrubwren	0	3.0	0	6.0	0	89.8	0	0	0	0.6	0.6	0	0	0
White-eared Honeyeater	9.4	56.6	7.1	7.5	0	0	0	0.9	0	16.0	0.5	0	1.9	0
White-naped Honeyeater	5.0	53.5	0.9	24.8	0	0	0	14.1	0	1.6	0.2	0	0	0
White-throated Treecreeper	73.4	22.5	3.8	0	0	0	0	0	0	0	0	0.3	0	0
White-winged Chough	0	0	0	0	0	100.0	0	0	0	0	0	0	0	0
Yellow-rumped Thornbill	0	0	0	0	0	100.0	0	0	0	0	0	0	0	0